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Department of Forestry, University of Kentucky,
Lexington, Kentucky, USA

Characteristics and ecological relationships of earthworm assemblages in undisturbed forest soils in the southern Appalachians of Kentucky, USA

D. B. Dotson and P. J. Kalisz

With 6 figures

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1. Introduction

Little is known about the earthworm fauna of undisturbed forest soils south of the limits of Quaternary glaciation in the eastern United States. Past research performed in this region has dealt primarily with problems of anatomy (e. g., Vail, 1972) and taxonomy (e. g., Gates, 1972, 1974; Reynolds, 1977), or has been directed towards constructing species lists (e. g., Reynolds, 1972; Reynolds *et al.*, 1974). Because of the objectives of such research, emphasis has not been placed on sampling undisturbed locations or on elucidating natural patterns of species occurrence and ecological relationships.

The present study was designed to address 2 fundamental questions concerning earthworm populations in the southern Applachians: 1. What is the nature of the earthworm fauna occuring in undisturbed forest soils? 2. Are there any relationships between the occurrence or abundance of earthworm species and the types of forest communities or soils? To examine these questions, research was performed on an experimental forest where vegetation and soils have been little disturbed, and where the locations, dates, and types of past activities are well documented. The guiding philosophy of this work was to examine remote and undisturbed sites in order to describe natural earthworm populations and ecological relationships.

2. Materials and methods

2.1. Study area

This study was conducted on the University of Kentucky's Robinson Forest in eastern Kentucky (37° 27′N, 83° 8′W). The climate is temperate humid continental. Average annual precipitation is 117 cm and is evenly distributed throughout the year. Mean annual temperature is 13 °C, and mean daily maxima and minima are 8 and −4 °C for January and 31 and 18 °C for July (Hill, 1976). Weather during the nine-month duration of the study was normal.

Robinson Forest lies within the Rugged Eastern Area of the Cumberland Plateau (Fenneman, 1938) of the southern Appalachians. Ridgetops and stream bottoms are narrow, and slopes with gradients >40 % occupy ~80 % of the land area. Geologic substrate consists of horizontally interbedded sandstone, siltstone, shale, and coal of the Breathitt Formation, Lower and Middle Pennsylvania Series (McDowell *et al.*, 1981).

Soils on the study area are well drained and formed chiefly in colluvium and residuum from sandstone and, less frequently, in finer-textured residuum from siltstone and shale. Profiles are similar to the Typic Hapludults, Typic Dystrochrepts, and Typic Haplumbrepts of the taxonomic system of the U. S. Department of Agriculture (USDA). Surface textures are sandy loam to silt loam, and coarse fragments (particles >2 mm) account for 10 to 86 % of the surface soil mass. All soil horizons are acid (range, *p*H 4.1 to 6.4), and A horizon thickness ranges from 0 to 27 cm.

The study area is in the Mixed Mesophytic Forest Region of Braun (1950). Relative basal areas of trees >15 cm in diameter at 1.4 m above ground (DBH) range from 100 % oak (*Quercus sp.* L.) to 0 % oak and 86 % a mixture of yellowpoplar (*Liriodendron tulipifera* L.), basswood (*Tilia heterophylla* Vent.), black cherry (*Prunus serotina* Ehrh.), and sugar maple (*Acer saccarum* Marsh.). Forests on lower slopes were heavily cut about 1920. From 1957 to 1972 a ridge-top road system was constructed, and forests were partially cut in a 60-m-wide band centered on the roads. Stand basal areas generally range from 20 to 25 $m^2 \times ha^{-1}$, and ages from 50 to 70 years.

2.2. Field methods

25 sites (fig. 1) representing the full range of forest communities found in the area were selected from 63 plots used in a forest inventory of 2 adjacent second-order watersheds (Overstreet, 1984). Approximate inventory plot centers were located in the field, and random azimuths and distances were used to select sampling sites within 10 m of the plot centers. Each sampling site consisted of three points arranged as an equilateral triangle with 1-m-long sides. These 3 points corresponded to the location for spring, summer, and winter earthworm samplings at each site.

A 27- by 27-cm frame was used to remove samples of the forest floor (0e horizon), and of increments of soil at 0 to 10, 10 to 20, 20 to 30, and 30 to 50 cm. Samples were spread in a pan, and earthworms were hand sorted and placed in containers of soil for transport to the laboratory. During the spring and summer sampling periods, the entire forest floor was retained for determination of mass, and subsamples of each soil depth, including sealed samples for moisture determination, were collected. During the winter, samples of the mineral soil were not collected, and the litter layer (L-layer) of the forest floor was collected. After the soil was sampled to a depth of 50 cm, approximately 4 l of 0.5 % formalin was poured into the bottom of the sample pit in an attempt to extract deeper-burrowing worms. This latter procedure failed to extract even a single earthworm over the course of this study and hence will not be mentioned further. The abundance of roots and stones, together with the need for careful hand sorting and extraction of undamaged specimens, caused the field procedures to be time consuming. Sampling time in the field for a single 27- by 27- by 50-cm pit averaged 4 h; it ranged from 3 h for coarser-textured soils with thin forest floors to 5 h for fine-textured or stony soils with thick forest floors.

Ground coverage by herbs, and other low-growing plants was quantified on each site during the spring by estimating foliage coverage by species through use of a 1-m^2 quadrat subdivided into 100 blocks; coverage for each site was an average based on three 1-m^2 quadrats centered on the 3 sampling points. Species and DBH of all trees >2.5 cm DBH were recorded within a circular plot, 5-m radius, surrounding the three sample points.

Following the winter sampling period, the 3 sampling pits on each site were enlarged to expose a single profile extending to bedrock or to a maximum depth of 150 cm. Soil morphology was described for these pits by using standard USDA procedures and nomenclature.

2.3. Laboratory methods

Earthworm color, behavior, and general morphology were recorded prior to anesthetization with 10 % EtOH. Length and three diameter measurements were recorded for anesthetized worms, then specimens were fixed in 4 % formalin and stored in 80 % EtOH (Ljungström, 1970). Earthworms were identified to genus for *Diplocardia* Garmon and for immature specimens of genera other than *Komarekiona*; identification was to species for *Komarekiona eatoni*

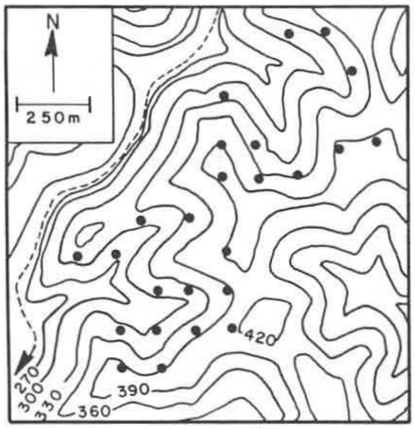

Fig. 1. Locations of the 25 study sites. Contour lines show elevation above sea level (meters), and dashed line shows the location and direction of flow of a major stream.

Gates, and for mature specimens of other genera. Examples of mature and immature specimens of all taxa recognized were sent to W. M. Fender (Soil Biology Associates, McMinnville, Oregon, USA) for confirmation of our identifications. In reporting results of this study, the various species of *Diplocardia* are not separated, and immature specimens of *Eisenoides* Gates are assumed to be *Eisenoides carolinensis* Michaelsen, the only species of this genus identified on the study area.

2.3.2. Soils

Forest floor samples from the spring and summer collections were ovendried at 60 °C and ashed at 450 °C to estimate organic mass. Fresh leaf litter from the winter sampling was separated by species and ashed; as described later, the relative mass of leaf litter by individual tree species was used as a measure of species influence on the various sites.

Chemical and physical analyses were performed on the spring and summer samples of the various mineral soil increments. Particle-size analysis was performed by the hydrometer method (Gee & Bauder, 1986) following removal of organic matter with NaOCl. Total nitrogen was determined by the Kjeldahl procedure (Bremner & Mulvaney, 1982), and organic carbon by the Walkey-Black procedure (Nelson & Sommers, 1982). Available calcium, magnesium, potassium,and phosphorus were estimated with the Mehlich 3 extractant (Mehlich, 1984). All element concentration in mineral soils are expressed on an air-dry basis for the fine-earth fraction (particles <2 mm); forest floor masses are on an oven-dry, ash-free basis.

2.4. Data analysis

Dry tissue mass per unit ground area and to a depth of 50 cm was used as the primary measure of earthworm importance in this study. An independent sample of 45 earthworms was used to develop a regression equation relating volume to dry mass. These earthworms were kept on moist filter paper until gut contents were completely voided, then volumes were estimated as cylinders based on anesthetized lengths and the averages of three diameter measurements. After drying at 103 °C, worm dry mass was linearly related to volume by least squares analysis: $DM = 9.14 + 0.13VOL\ (r^2 = 0.88)$, where DM is dry mass (mg) and VOL is volume (mm^3). To estimate earthworm dry mass on the study sites, the volume of each of the 245 specimens collected was calculated as described above, and dry mass was determined by using the regression equation. Total earthworm dry mass collected in each 27- by 27-cm quadrat was then expanded to a 1-m^2 basis.

Relative mass by species of leaf litter in the L-layer of the forest floor sampled in winter was used as a measure of the importance of individual tree species on each study site. This measure of importance considers not only the tree species that overhang the site but also the possibility that leaf litter is redistributed over the ground after fall.

Nonparametric statistical methods were used in all analyses since the data did not satisfy the assumptions of normal statistics even after transformations. The significances of the differences in earthworm density and dry mass per unit ground area, of the mass of individual earthworms, and of the depth of occurrence were tested among the various taxa or among the 3 sampling seasons with Kruskal-Wallace and Mann-Whitney tests. Relationships between earthworm dry mass and various soil and vegetation properties were examined by using Spearman's rank correlation analysis. In some cases, significant correlations are illustrated with the Robust Locally Weighted Regression (LOWESS) method of Cleveland (1979) to graph trend lines; in these cases, trend lines presented on graphs are not computationally related to the Spearman correlation coefficients presented in table 2.

3. Results

3.1. Species assemblages

Earthworms were not found on 2 sites during any sampling season. Of the remaining 23 sites, 22 were inhabited by assemblages consisting entirely of taxa native to southeastern United States. Two undescribed (W. M. Fender, personal communication, 1987) species of *Diplocardia, Komarekiona eatoni*, and *Eisenoides carolinensis* were the most widely distributed and important species (table 1). A single individual of *Bimastos longicinctus* Smith et Gittens was collected, and *B. zeteki* Smith et Gittens was observed in the study area but not within a sampling plot.

Three specimens of *Octolasion tyrtaeum* Savigny were on one site during the summer and winter sampling periods. The occurrence of this exotic species was related to nearby disturbance surrounding a small abandoned shaft used briefly, 20 to 25 years previously, to mine coal by hand. *Octolasion tyrtaeum* seemed to be established along the abandoned road in the immediate vicinity of the

Table 1. Seasonal summary of population characteristics for three dominant earthworm taxa.

Species	Occurrence			Importance			Clitellate		
	Spr	Su	Wi	Spr	Su	Wi	Spr	Su	Wi
					%				
Diplocardia spp.	72	56	76	80	62	83	16	25	30
Komarekiona eatoni	44	44	28	9	12	7	7	21	7
Eisenoides carolinensis	36	40	24	9	24	8	0	12	71

Note: "Occurrence" is in terms of percentage of plots; "Importance" in terms of percentage of biomass; and "Clitellate" in terms of percentage of individuals.

mine and had apparently spread from there into the sampling plot, which is downslope approximately 50 m horizontal distance.

3.2. Abundance of major species

Median earthworm population densities over all 25 plots were 41, 27 and 27 individual m^{-2}, respectively, in spring, summer, and winter; median dry masses were 1.8, 1.4 and 3.1 $g \times m^{-2}$ over the same 3 seasons (fig. 2). Density and dry mass per unit area were not statistically different among seasons. Dry mass per individual was, however, significantly greater in winter (median mass, 61 mg) than in summer ($P = 0.002$; 33 mg) and spring ($P = 0.007$; 34 mg) (fig. 2). This latter result was due to the more common occurrence of large clitellate individuals of *Diplocardia* sp. and of *E. carolinensis* in the winter collection (table 1).

Diplocardia sp. was overwhelmingly dominant in the study area, accounting for 60 % of the total number of earthworms and 77 % of the total biomass collected over the duration of this study. *Komarekiona eatoni* and *E. carolinensis* were similar in occurrence and importance (table 1) and together accounted for 22 % of the total biomass collected. The latter 2 species accounted for a higher proportion of the earthworm mass collected during the summer (table 1), perhaps due to burrowing by *Diplocardia* below the 50-cm depth of sampling.

Examined over the 3 sampling periods, the 3 dominant species had distinctly different depth distributions. *Diplocardia* sp. was a relatively deep burrower, with 89 % of its mass occurring below a depth of 10 cm and 46 % below 20 cm (fig. 3). In contrast, the masses of *K. eatoni* and *E. carolinensis* were concentrated in the surface soil, with 64 % and 83 %, respectively, above a depth of 10 cm, and only 8 % and 1 % below 20 cm (fig. 3). *Eisenoides carolinensis* was the only species found regularly in the forest floor (fig. 3); 81 % of the mass of this species collected in the spring was in this horizon. *Eisenoides carolinensis* was also observed traveling over the ground surface during wet weather.

3.3. Earthworm-Environment relationships

There was no relationship between earthworm biomass and any of the following soil physical properties measured in the various soil sampling increments: gravimetric water percentages in the spring (range, 13–28 %) or in the summer (range, 7–24 %); coarse fragment concentration (range, 10–95 %); sand concentration (range 5–71 %); silt concentration (range, 2–84 %); clay concentration (range, 0–41 %).

Dry mass of earthworms was significantly correlated with a number of soil chemical properties (table 2; fig. 4). In general, dry mass increased with conventional measures of soil fertility such as *p*H and total N (fig. 4). Correlations were strongest and most consistently significant when relating the

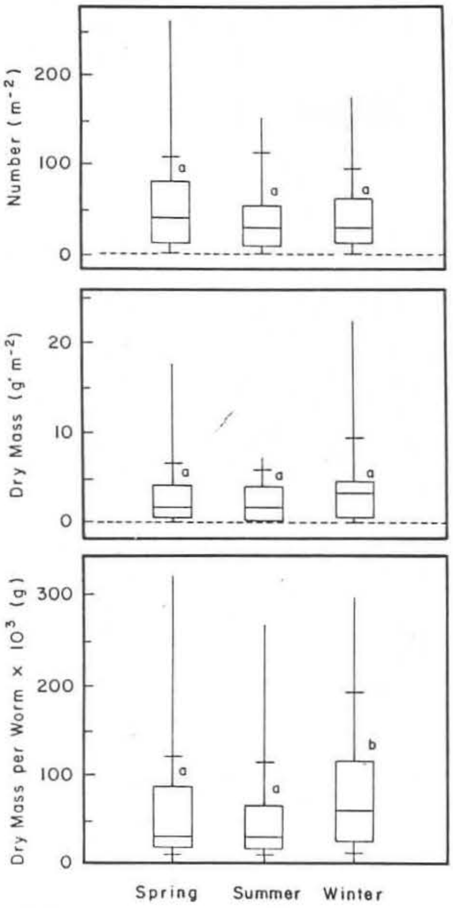

Fig. 2. Distributional summary of earthworm numbers per unit ground area, and dry mass per unit ground area and per individual for 3 sampling seasons. Upper, center, and lower horizontal lines of the box indicate, respectively, the 75th, 50th, and 25th percentiles; uppermost and lowermost horizontal lines indicate, the 90th and 10th percentiles; upper and lower vertical lines point to the 99th and 1st percentiles. For each variable, seasonal distributions marked with the same letter are not statistically different at the 0.05 level; n = 25 plots. Sampling depth was 50 cm.

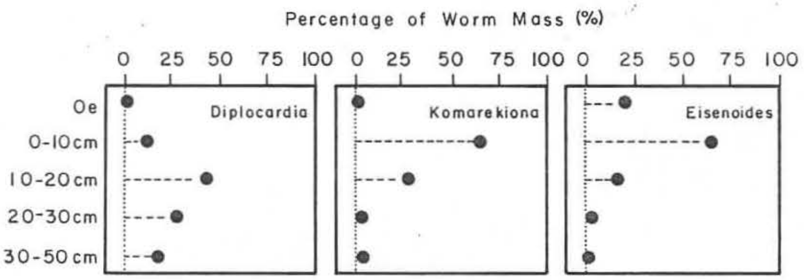

Fig. 3. Depth distribution of the dry biomass of 3 dominant earthworm genera.

dry mass of earthworms collected from the 0- to 50-cm depth to the chemical fertility of the 0- to 10-cm depth (table 2). Organic C concentrations in the 0- to 10-cm soil depth were moderately high on all of the 25 sample sites (ranged from 26- to 84 $g \times kg^{-1}$, with a median of 48 $g \times kg^{-1}$); because of uniformly high C concentrations, there was no relationship between earthworm biomass and C concentration in the 0- to 10-cm depth (table 2). In contrast, C concentration in the 10- to 20-cm depth was significantly correlated with biomass (table 2; fig. 4). This latter depth increment corresponds to a transitional zone (AB horizon) between the overlying A and the underlying B. Morphologically, the AB horizon was distinguished by Krotovina-like patterns of dark and light colors that seemed due to burrowing and downward mixing of organic materials by earthworms and other soil animals.

Table 2. Nonparametric correlations between earthworm dry mass collected in the 0- to 50-cm depth and soil chemical variables in 4 soil depth increments.

Variable	Spearman Correlation Coefficient (P)			
	0 – 10cm	10 – 20cm	20 – 30cm	30 – 50cm
*p*H	0.65 (0.0004)	ns	ns	ns
Extractable Ca	0.62 (0.0008)	0.71 (0.0001)	0.70 (0.0001).	0.69 (0.0002)
Extractable Mg	0.67 (0.0002)	0.51 (0.01)	0.42 (0.03)	ns
Extractable K	0.53 (0.006)	ns	ns	ns
Extractable P	0.55 (0.004)	ns	ns	ns
Organic C	ns	0.42 (0.04)	ns	ns
Total N	0.57 (0.003)	0.51 (0.009)	0.42 (.04)	ns
C/N	−0.73 (0.0001)	−0.57 (0.003)	ns	ns

Note: Significance levels (P) are in parentheses, and "ns" indicates $P \geq 0.05$; $n = 25$ plots.

Earthworm biomass was negatively related to the mass of unincorporated organic material contained in the forest floor (0e horizon) ($r = -0.76$; $P = 0.0001$) and positively related to the thickness of the A horizon ($r = 0.57$; $P = 0.003$) (fig. 5). Earthworms were most important in soils with A horizon thicknesses of 10 to 15 cm and Oe horizon masses of 500 to 750 $g \times m^{-2}$ (i.e., in soils with well-developed mull humus layers).

As the relative contribution of oak trees to leaf litter input on a site declined, earthworm mass increased ($r = -0.59$; $P = 0.002$) (fig. 6). Sites with low oak litter input were dominated by mesic tree species such as yellowpoplar, basswood, sugar maple, and black cherry. Non-oak plots were also characterized by relatively high densities of herbs and ferns, and earthworm mass was positively correlated with percentage herbaceous ground coverage ($r = 0.63$; $P = 0.008$) (fig. 6). Ground coverage by *Dentaria diphylla* MICHX. (Cruciferae) ($r = 0.54$; $P = 0.005$), and *Anemonella thalictroides* L. and *Thalictrum* L. spp. (Ranunculaceae) ($r = 0.51$; $P = 0.009$) were especially well correlated with earthworms mass; high worm biomass was also associated with the occurrence of *Sanguinaria canadensis* L. (Papaveraceae), *Ozmorhiza claytoni* MICHX.) CLARKE (Umbelliferae), *Polystichum acrostichoides* (MICHX.) SCHOTT (Polypodiaceae), and *Disporum lanuguinosum* (MICHX.) NICHOLSON (Liliaceae). Sites with low earthworm biomass were characterized by a canopy layer dominated by *Quercus coccinea, Q. prinus,* and *Q. rubra;* by little herbaceous ground cover; and by relatively well-developed low (<50 cm tall) understory of tree seedlings and shrubs. Earthworm mass was negatively correlated ($r = -0.60$, $P = 0.002$) with ground coverage by foliage of this low woody understory.

4. Discussion

Except for a single sampling location near a point of disturbance, the earthworm fauna within the 93-ha area of the 2 study watersheds was composed entirely of native species. Excavations throughout the Robinson Forest have supported the patterns documented on the study area: assemblages of native species occupy undisturbed forest soils, and exotic earthworms occur on limited areas of intense

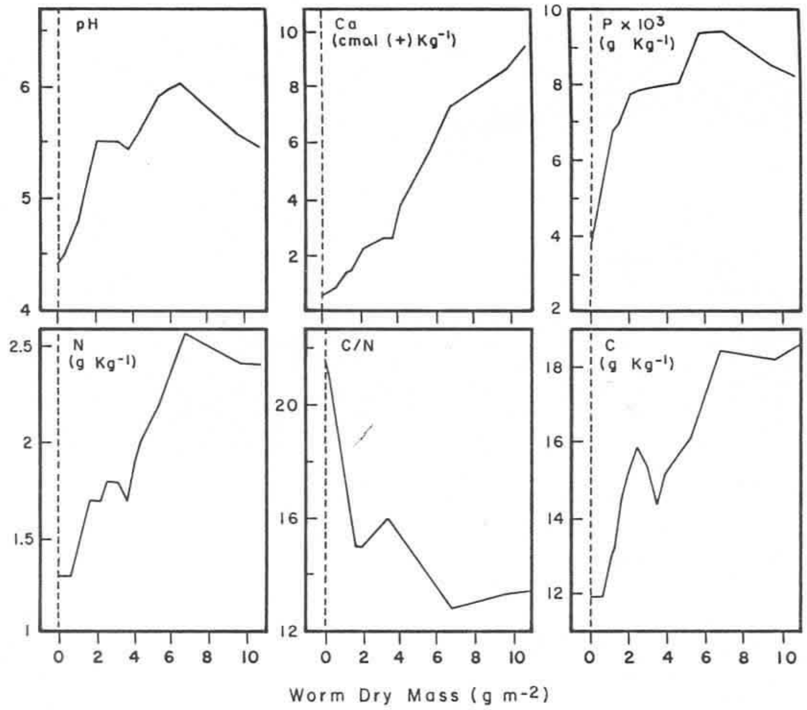

Fig. 4. Robust Locally Weighted Regression (LOWESS) lines illustrating relationships between earthworm dry mass in the 0- to 50-cm depth and various soil chemical parameters. All soil parameters are for the 0- to 10-cm depth except C is for the 10- to 20-cm depth.

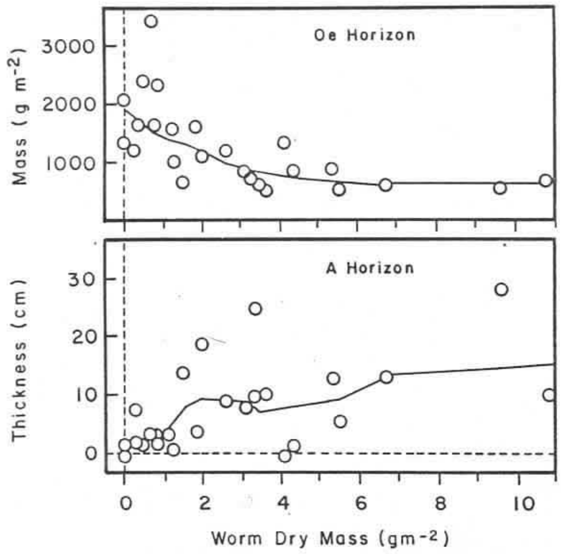

Fig. 5. Scatterplots and Robust Locally Weighted Regression (LOWESS) lines illustrating relationships between earthworm dry mass in the 0- to 50-cm depth and: 1. Oe horizon mass; 2. A horizon thickness.

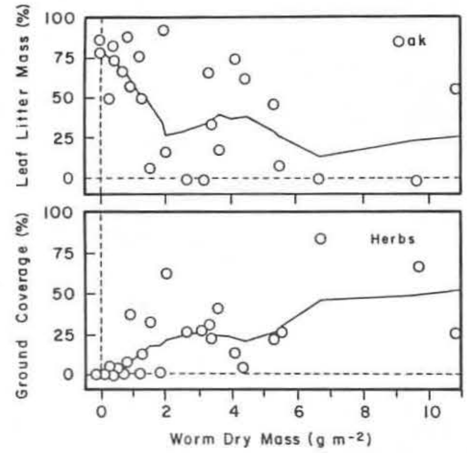

Fig. 6. Scatterplots and Robust Locally Weighted Regression (LOWESS) lines illustrating relationships between earthworm dry mass in the 0- to 50-cm depth and: 1. contribution of *Quercus* spp. to leaf litter mass; 2. ground coverage by herbs.

disturbance of deforestation. To our knowledge, this is the first study that documents the extensive occurrence of native earthworm species assemblages in the southern Appalachians. Possibly due to sampling of disturbed areas, other studies of forest soils in the region have generally reported mixtures of native and exotic species, or totally exotic earthworm faunas (e. g., REYNOLDS, 1972; REYNOLDS *et al.*, 1974).

The 2 species of *Diplocardia* collected on the study area were undescribed (W. M. FENDER, personal communication, 1987), and the local diversity of this dominant genus is unknown. Diversity may, however, be great since the study area lies south of the Quaternary glacial limits in an area that may have served as a faunal refuge (GATES, 1970). *Komerekiona eatoni,* a little known and only recently described species (GATES, 1974; REYNOLDS, 1977), and *Eisenoides carolinensis* were generally distributed over the study area (table 1); *Bimastos* spp. were much less frequently collected. These 4 native genera – *Diplocardia* (Acanthodrilidae); *Komarekiona* (Komarekionidae); *Eisenoides* and *Biomastos* (Lumbricadae) – represent 3 distinct megadrile families and characterize the endemic earthworm fauna of the Quaternary refugium in the southeastern United States (GATES, 1972, 1974). Abundance and biomass per unit ground area determined for these native earthworms in the present study were in the low ends of the ranges reported for deciduous forest soils in other parts of the world (LEE, 1985).

Observations of feces made during the preservation process suggest that *Diplocardia, K. eatoni,* and *E. carolinensis* are dominantly humus-feeders (*sensu* PEREL, 1977). Based on depths of occurrence (fig. 3), the lack of pigmentation, and relatively large size, *Diplocardia* sp. and *K. eatoni* may be classified as endogees (*sensu* BOUCHÉ, 1977). *Eisenoides carolinensis,* on the other hand, sometimes occurs in the 0e horizon (fig. 3), occasionally ingests poorly humified material, and is darkly pigmented. Based on these characteristics, *E. carolinensis* is probably best classified ecologically as a epiendogee (*sensu* BOUCHÉ, 1977).

The 2 sites that lacked earthworms were located on upper slopes of south-west facing noses, and hence might predictably represent poor earthworm habitat. Among the remaining 23 sites, earthworm biomass was greatest in hollows and lower slope positions with mixed forests, abundant herbs, relatively thick A horizons, thin 0e horizons, and high chemical fertility. Conversely, areas with low earthworm biomass were characterized by dominance of *Quercus* spp. in the tree canopy with a low woody ground cover, by relatively low chemical fertility, and by slow litter incorporation and decomposition as indicated by high Oe horizon masses and C/N ratios (table 2; fig. 4–6). Although bounded by these contrasting situations, earthworm mass and the various soil and vegetation characteristics were only moderately well correlated (table 2). This is likely due to the fact that soil and vegetation characteristics varied only over a limited range; extreme contrasts in vegetation (e.g., coniferous *versus* deciduous trees) were lacking, and soil properties (e.g., *p*H, fig. 4) were generally within limits thought to be suitable for earthworms. In addition, unlike the well-documented case of selective feeding on leaf litter by *Lumbricus terrestris* L. (Satchell & Lowe, 1967), the dominant taxa on the study area seemed to be primariy humus feeders, and hence might exhibit low sensitivity to the nature of the plant species occupying an area.

The characteristics of earthworm populations native to southeastern North America are poorly documented. Although determination of diversity in terms of number of species, especially for the genus *Diplocardia*, must await further taxonomic work, the results of the present study show that unique and relatively diverse earthworm assemblages occur in association with rich mull forest soils in the study area and probably throughout the southern Appalachians. The cause-and-effect nature of this relationship is no doubt reciprocal: inherently favorable soils and landscape positions support larger and more diverse earthworm populations, while thriving earthworm populations, even when dominated by subsoil species (Scheu, 1987), contribute to the development of rich mull humus layers.

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Earthworms were collected during the spring, summer, and winter seasons on 25 saites representing the full range of forest communities found on an experimental forest in the Appalachians of eastern Kentucky, USA. Earthworms were hand sorted from volumetric soil samples 27- by 27-cm in horizontal area and 50 cm deep. Earthworms were not found on 2 of the 25 sites and, except for the occurrence of 3 individuals of *Octolasion tyrtaeum* Savigny on a single site near a point of disturbance, all of the 245 specimens collected were from taxa native to the southeastern United States. The earthworm fauna was overwhelmingly dominated by 2 undescribed species of *Diplocardia* Garman, and also included the genera *Eisenoides* Gates, *Komarekiona* Gates, and *Bimastos* Moore. These 4 genera represent 3 distinct megadrile families native to the eastern United States south of the limits of Quaternary glaciation.

Earthworm biomass increased with increases in conventional measures of soil fertility, A horizon thickness, and herbaceous ground coverage. Biomass decreased with increases in 0 horizon mass and with increases in importance of *Quercus* L. spp. as a source of leaf litter. Biomass and abundance of earthworms did not differ significantly among seasons; median dry biomass and abundance were 1.9 $g \times m^{-2}$ and 36 individuals m^{-2}, respectively.

Key Words: Acanthodrilidae, Appalachians, deciduous forests, Komarekionidae, Lumbricidae, native earthworms, Oligochaeta, soil properties.

Address of the authors: D. B. Dotson and P. J. Kalisz (corresponding author), Department of Forestry, University of Kentucky, Lexington, Kentucky 40546-0073, USA.